

Discovery of an acoustically locating parasitoid with a potential role in divergence of song types among sympatric populations of the bush cricket *Mecopoda elongata*

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Abstract

The bush cricket *Mecopoda elongata* provides a striking example of sympatric intraspecific divergence in mating signals. Five completely distinct song types are found in various parapatric and sympatric locations in South India. While there is convincing evidence that population divergence in *M. elongata* is being maintained as a result of divergence in acoustic signals, cuticular chemical profiles, and genital characters, the causes of the evolution of such divergence in the first place are unknown. We describe the discovery of a tachinid parasitoid with an orthopteroid hearing mechanism affecting *M. elongata*. This parasitoid may have a role in driving the extraordinary divergence that had occurred among *M. elongata* song types. Over two years we sampled individuals of three sympatric song types in the wild and retained individuals in captivity to reveal rates of parasitization. We found that all three song types were infected with the parasitoid but that there were significant differences among song types in their probability of being infected. The probability of tachinid parasitization also differed between the two sampling periods. Therefore, it is possible that parasitoid infection plays a role in song type divergence among sympatric bush cricket populations.

Keywords

cryptic species, katydid, speciation, Tachinidae

Introduction

In host-parasite coevolution, hosts evolve mechanisms to avoid parasite attack and parasites evolve counter-mechanisms to detect and infect hosts efficiently. Instances of insect parasitoids, whose larvae parasitize their host for nutrition and development, eventually causing the death of the host, are abundant in nature (Godfray and Shimada 1999, Santos and Quicke 2011). They mostly belong to the order Hymenoptera (78%) or to the family Tachinidae, order Diptera (20%) (Feener and Brown 1997, Godfray and Shimada 1999). Each host species is typically parasitized by 2–8 parasitoid species and hosts for each parasitoid tend to be closely related species (Santos and Quicke 2011). Parasitoids can be grouped into idiobionts or koinobionts depending on the host's ability to live

after being parasitized (Santos and Quicke 2011). Typically, unlike idiobionts, most koinobionts are endoparasites that affect young hosts, have longer developmental stages, and a shorter adult life. They are normally pro-ovigenic and have a smaller host range compared to ectoparasitic idiobionts (Santos and Quicke 2011). Widely distributed tachinids are parasitoids on a variety of insect orders including Lepidoptera, Orthoptera, Coleoptera, Hymenoptera, Heteroptera, and many others (Feener and Brown 1997, Stireman et al. 2005, Cerretti et al. 2014) due to the ability of their larvae to avoid host immune responses (Feener and Brown 1997). Such a koinobiont tachinid parasitoid that exploits its orthopteran hosts' acoustic communication is the subject of this study.

Tachinid parasitoids (especially of tribe Ormiini) have evolved to take advantage of intraspecific acoustic communication particularly in orthopteran and hemipteran species (Lehmann 2003, Lakes-Harlan and Lehmann 2014). Early studies to identify this phenomenon of acoustic exploitation found that females of the tachinid fly *Euphasiopteryx ochracea* (now, *Ormia ochracea*) showed phonotaxis to song playback of the field cricket *Gryllus integer* (Cade 1975). *O. ochracea* females were also found to be more attracted to host male choruses than to single host callers (Cade 2010). *O. ochracea* females bear orthopteroid hearing organs (featuring a prominent pressure sensitive tympanum exposed to the air but receiving sound from both sides), which are most sensitive in the 4 to 6 kHz range, corresponding to the dominant frequency range of the calls of one of their hosts, *Gryllus rubens* (Robert et al. 1992). Parasitoid infection affects the male host's calling ability, which gradually declines until his death (Cade 1984).

Calling and chorusing behavior in orthopterans is thought to have evolved under selection to avoid exploitative parasites or predators (Greenfield 1983, Cade and Wyatt 1984, Henry 1994). Currently, the two most studied dipteran parasitoid groups are tachinids belonging to tribe Ormiini and sarcophagids belonging to tribe Emblemastomatini, parasitizing crickets and bush crickets (Orthoptera) and cicadas (Hemiptera), respectively, with the help of independently evolved hearing mechanisms (Hedwig and Robert 2013, Lakes-Harlan and Lehmann 2014). The sarcophagid

genus *Emblemasoma* has been found to target cicada males calling during the day (Farris et al. 2008).

In contrast, 68 species belonging to the Ormiini tribe of the Tachinidae family are predominantly parasitoids that can acoustically locate bush cricket hosts that call at night (Lehmann 2003). For example, *Therobia leonidei* (a tachinid parasitoid) locates its tettigoniid (*Poecilimon* sp.) host males by eavesdropping on their calls (Lakes-Harlan and Heller 1992). Other similar host-dipteran parasitoid systems include the bush cricket *Neoconocephalus robustus* and tachinid *Ormia brevicornis*, the bush cricket *Scapteriscus vicinus* and tachinid *Ormia depleta*, the bush cricket *Orocharis luteolira* and tachinid *Ormia dominicana*, the bush cricket *Sciarasaga quadrata* and tachinid *Homotrixa alleni*, the cicada *Okanaga rimosa* and sarcophagid *Colcondamyia auditrix* (Cade 1984), and many others (reviewed in Feener and Brown 1997, Zuk and Kolluru 1998, and Lehmann 2003). Here we describe our observation of a tachinid parasitoid infecting an orthopteran host, *Mecopoda elongata*. This system is of particular interest because the mate-attracting auditory signals exploited by the parasitoid also form the basis of an intra-specific reproductive isolating mechanism that has been implicated in incipient speciation in this group (Dutta et al. 2017).

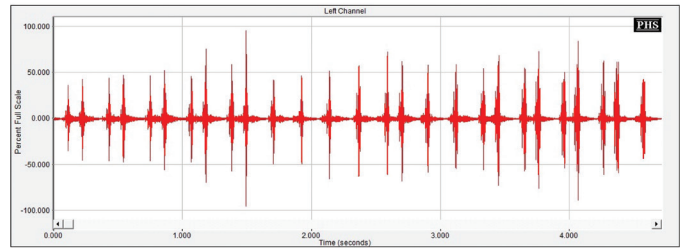
The bush cricket species *Mecopoda elongata* can be divided into five song types that are morphologically very similar (Nityananda and Balakrishnan 2006). These song types show subtle differences in genital morphology and cuticular lipid profiles (Dutta et al. 2018) and females of one of the song types, Chirper, show a strong preference for their own call type (Dutta et al. 2017). There appear to be only a few records of known tachinid parasitoids parasitizing lepidopterans in India (Sathe 2012, Shendage and Sathe 2012), but there has been no published evidence of tachinid parasitoids affecting *M. elongata* males or any calling orthopteran species from India that we are aware of (Crosskey 1976). India has many tachinids (>140 species), as well as 1033 described orthopteran species/subspecies within 398 genera and 21 families consisting of mostly acoustically communicating crickets and bush crickets (Gryllidae and Tettigoniidae) (O'Hara et al. 2009, Chandra and Gupta 2013). In this study, we describe a hitherto unknown relationship between a tachinid fly and three distinct song types of *M. elongata*. These three song types differ considerably in their temporal features (Fig. 1). However, the spectral features (for example, dominant frequency) of their songs appear similar (Nityananda and Balakrishnan 2006). Since the evolutionary origins of these song types are unknown, the potential for acoustically orienting parasitoids to have played a role in their divergence is an obvious point of interest.

The objectives of our study were 1) to describe the tachinid parasitoids affecting *M. elongata* populations and 2) to determine whether there were any differences in the prevalence of parasitoid infection among *M. elongata* song types.

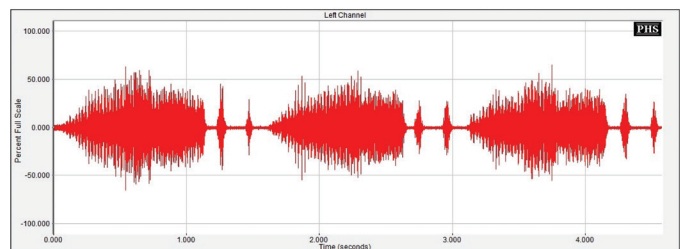
Methods

Field sampling was carried out in Kervashe, Hurabi, and Heringe locality around Kadari field station (13°13'N, 75°05'E), Karnataka, India. Adult *M. elongata* males were collected opportunistically from the three sites between January and March each year for a period of two years (2013–2014). The sampling took place between 7:30 pm and 9:30 pm at night on at least two dates for a given location each year. *M. elongata* males were identified as Double Chirper, Two Part, and Helicopter by listening to their calls and recording them when possible. While Double Chirper calls consist of only chirps and Helicopter calls

Double Chirper



Two-Part



Helicopter

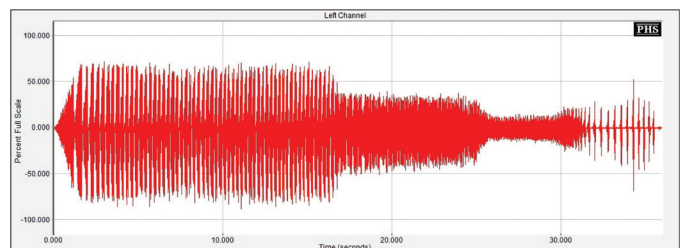


Fig. 1. Oscillograms showing distinct temporal features of the three *M. elongata* song types: Double Chirper, Two Part, and Helicopter.

consist only of trill, Two Part consists of both chirp and trill components (Fig. 1). *M. elongata* males that were captured were housed individually in plastic boxes (15 cm × 7 cm × 5 cm) and fed *ad libitum* on oat flakes (Quaker Oats, Morten Seeds & Grains Pty. Ltd.), fish food (Taiyo Grow, Taiyo Petproducts [P] Ltd.) and water. These males were observed over subsequent days for parasitoid infection. An *M. elongata* male was considered infected if it was found dead inside the plastic box along with presence of an ovoid tachinid pupa.

There is general agreement over the classification of the family Tachinidae (Stireman et al. 2005) into either four (Wood 1987) or five subfamilies (Crosskey 1976). Between these two alternative classificatory schemes, the subfamily Tachininae appears consistently as a taxonomic group in both but forms a diverse group in many respects and is probably not monophyletic (Cerretti et al. 2014). The classifications of groups within the Tachininae is incomplete and awaits further refinement, which will benefit from better information about their reproductive behavior (oviposition methods, host location, and selection) and ecology (host utilization and life history). We used a Leica M165C microscope to identify the fly as tachinid and took photographs of important characters presented in this study using a Leica DFC290 digital camera fitted to this microscope. Diagnostic features of the Tachinidae (Crosskey 1976) that appear on the newly discovered fly are as follows:

1. Adults have subscutellum and meral bristles.
2. First instar larvae do not have mandibles or they are vestigial.
3. Anterior cephalopharyngeal skeleton appears as a hook or axe-like beak.

We used a generalized linear modelling (GLM) framework to analyze categorical predictors (song type, location, year, and their interactions) with potential associations with tachinid infection. This approach allowed us to examine potential interactions between song type and predictors as well as their potential independent effects on parasitization probability. Tachinid infection was modelled as a binary variable using logit as a canonical link function with infected song type individuals assigned 1 and uninfected individuals assigned 0. Model 1 included song type, location, and year as linear predictors while model 2 also included the two-way interactions between song type, location, and year. By comparing the two models (model 1 AIC = 132.81, model 2 AIC = 140.7), we found that model 1 had the best fit (the difference in AIC values was more than 7 and the difference between null deviance and residual deviance was 81.67 with a loss of only 5 degrees of freedom), indicating that interactions between song type and other predictors were not important in explaining variation in parasitization probability.

Results

Morphology of the tachinid fly.—The tachinid fly found parasitizing *M. elongata* appears to belong to a single typical muscoid dipteran fly species of around 10 mm long (Fig. 2). It has a pair of red compound eyes and two distinct halteres (Fig. 2). The prothoracic auditory spiracles (AS) are enlarged and it has a typical furry peritreme (the integument that surrounds the spiracles) and clearly visible hairs on the anterior side (Fig. 3). It is a hearing tachinid (most likely belonging to the tribe Ormiini) featuring a hearing organ (a modified inflated prosternum) between its head and thorax on the ventral side (Fig. 4), with morphology and position similar to that of the well-studied ear of *Therobia leonidei* and *Ormia ochracea* (Lakes-Harlan and Heller 1992, Hedwig and Robert 2013). The prosternal tympanal membrane (PTM) is separated by a ridge from the coxa that is also large. The larva that comes out of an infected animal is 20 mm long and forms an ovoid pupa 10 mm long. The species-level identity of the tachinid fly could not be ascertained due to the unavailability of a dipteran/tachinid taxonomist in India and the stringent regulation of the export of biological material that prevented us from seeking an identification outside of India. However, our aim here was not primarily taxonomic; rather, it was to establish that all instances we found were of the same species and to examine its potential significance for the evolution of its *M. elongata* host.



Fig. 2. External morphology of tachinid parasitoid affecting *M. elongata* song types.

Our 2014 collection of *M. elongata* males included 11 infected individuals. The mean larval emergence time was 6.9 days (standard deviation = 1.64, range 5–10 days), which is typical for tachinid flies (Stireman et al. 2005). Larval emergence led to the death of *M. elongata* males, which often lived for some hours after larval emergence but died within the same day. In 9 out of 11 cases, a single larva emerged and in the remainder, 2 larvae emerged, suggesting a slightly lower rate of hosting multiple parasites than is found in *Ormia ochracea* infections of *Teleogryllus oceanicus* and some *Gryllus* species. Although the latter species typically harbor 1 to 2 larvae, they may support up to 8 larvae in extreme cases in *T. oceanicus* (Adamo et al. 1995, Kolluru and Zuk 2001). Of the 13

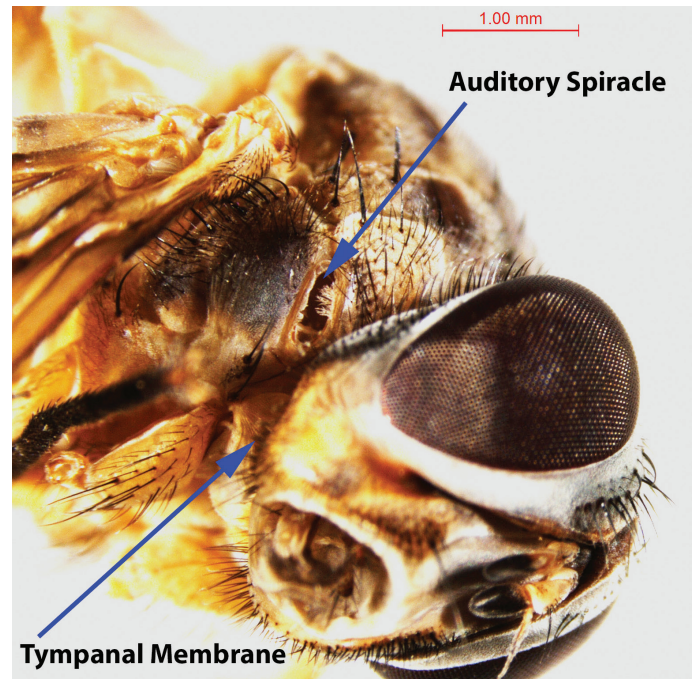


Fig. 3. Auditory spiracle encircled by peritreme and tympanal membrane of tachinid parasitoid affecting *M. elongata* song types.

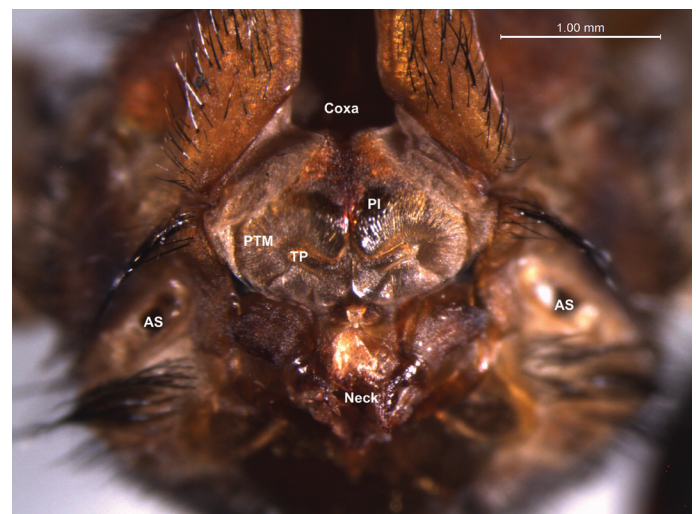


Fig. 4. Modified inflated prosternum acting as a hearing organ in tachinid fly affecting *M. elongata* song types. AS: auditory spiracle, PTM: prosternal tympanal membrane, TP: tympanal pit, and PI: prosternal inflation (Lakes-Harlan and Heller 1992, Hedwig and Robert 2013).

pupae observed in 2014, 8 emerged as adult flies after a mean of 11 days (standard deviation = 1.3, range 9–13 days). It was clear that all the parasites emerging in the lab were of the same species of tachinid, as described above.

Tachinid infection of different song types.—Over the two years of study (2013 and 2014), tachinid infections were found in all three *M. elongata* song types (Double Chirper, Two Part, and Helicopter) found at our collection sites (Fig. 5). Details of the *M. elongata* male samplings and recorded infection in percentages and sample size (n) are given in Table 1.

Analysis of deviance by F test on model 1 showed that song type ($F = 5.37$, $p = 0.00467$) and year ($F = 70.0$, $p < 0.0001$) both had significant effects on tachinid infection rate. However, sampling locations did not have any effect on the tachinid parasitization of *M. elongata* males, suggesting that instances of tachinid infection were similar in the three locations we sampled. GLM analysis also supported our finding that there was significantly higher parasitoid infection of all three *M. elongata* song types in the year 2013 (27 infected out of 47 = 57%) compared to 2014 (11 infected out of 173 = 6%). In the GLM analysis, we assigned Helicopter song type as the reference class for comparing tachinid infection probability with the other two *M. elongata* song

types. We found that when a sampled *M. elongata* individual was of the song type Two Part rather than Helicopter, there was an increasing probability of tachinid infection that was statistically significant (Wald z-statistic (z) = 2.002, $p = 0.0453$). However, when a sampled individual was Double Chirper rather than Helicopter, the probability of tachinid infection was not significantly different (Wald z-statistic (z) = 0.867, $p = 0.386$); i.e., Double Chirper and Helicopter did not differ in their probability of contracting tachinid infection. We, therefore, had evidence that song types differ in their probability of being parasitized with an indication that the Two Part song type was more likely to be parasitized than either Helicopter or Double Chirper song types at the locations we sampled.

Discussion

Tachinid flies (Stireman et al. 2005, Cerretti et al. 2014) have not been extensively studied and little is known about their evolution, ecology, and behavior (Stireman et al. 2005). The diversification of host use appears to have evolved after the acquisition of parasitoid life history since all known tachinids are parasitoids (Feener and Brown 1997, Lehmann 2003). This study is the first record of a paleotropical parasitoid affecting *M. elongata* males or any calling orthopteran species from India. This confirmation follows a recent anecdotal account of Malaysian *M. elongata* infected by larvae of a parasitoid fly belonging to family Tachinidae (Hartbauer et al. 2011). Although the distribution and abundance of *M. elongata* has not been systematically studied, preliminary opportunistic sampling in known *M. elongata* habitats indicates that there is possibility of a high proportion of the *M. elongata* population being infected by tachinid parasitoids. Our generalized linear model suggested that the probability of the parasitoid infection in *M. elongata* varied significantly between years and was dependent upon the song type of potential hosts. The sampling locations and the various interactions among predictors did not contribute to the parasitization likelihood.

Fifty seven percent (27 out of 47) of *M. elongata* sampled during 2013 were infected by the tachinid fly. This high rate of infection is also seen in the *Therobia leonidei*-*Poecilimon* parasitoid-host system (Heller and von Helversen 1993). At such high infection rates, there is inevitably strong selection on *M. elongata* from tachinid parasitoids with the potential for this to drive changes in acoustic signals that reduce detection probability (Hedwig and Robert 2013). The proportion of parasitoid-infected *M. elongata* individuals, however, drastically declined for the year 2014 (11/173 = 6%) suggesting a possible density dependent host-parasite interaction (although further study is needed to confirm this).

We found that all three song types (varying predominantly in their temporal characteristics) included some infected individuals, indicating that if the presence of parasitoids has influenced the evolution of song types, it has not allowed any of the song types that we studied to avoid parasitization completely. Parasitoids are known to exploit the spectral features of host songs that are generally conserved among closely related species (Lehmann 2003). Tachinids may be able to locate the different *Mecopoda* male songs by exploiting the dominant frequency of their call rather than the temporal features such as call structure and call rate. The different *M. elongata* song types do not differ strongly in dominant frequency (Nityananda and Balakrishnan 2006), a situation also observed among song types in *Therobia leonidei* (Lakes-Harlan and Heller 1992, Robert et al. 1992) that is parasitized by the tachinid *Homotrixa alleni*, which also fails to show any preference among the different hosts it parasitizes (Lehmann 2003).

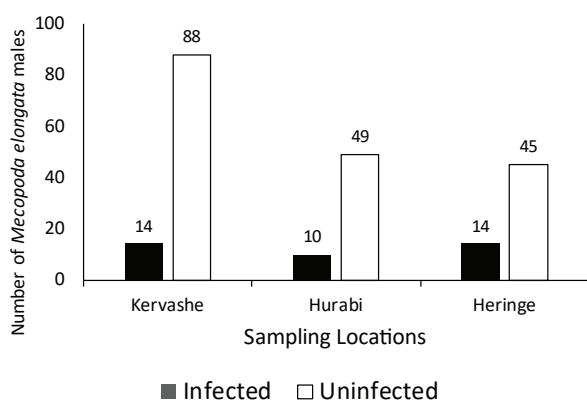


Fig. 5. The number of infected and uninfected *M. elongata* individuals sampled at the three different sampling sites within the two-year sampling period (2013–14).

Table 1. Sampling details of calling *Mecopoda elongata* males belonging to three song types that were collected from three different localities across two years leading to the discovery of tachinid parasitism.

Song type	Location	Year	Infected (%)	Uninfected (%)
Double Chirper	Kervashe	2013	47 (n=7)	53 (n=8)
	Heringe	2013	100 (n=3)	0 (n=0)
	Kervashe	2014	0 (n=0)	100 (n=56)
	Heringe	2014	0 (n=0)	100 (n=20)
	Hurabi	2014	13 (n=5)	87 (n=34)
Helicopter	Kervashe	2013	38 (n=5)	62 (n=8)
	Heringe	2013	73 (n=11)	27 (n=4)
	Kervashe	2014	0 (n=0)	100 (n=4)
	Heringe	2014	0 (n=0)	100 (n=17)
	Hurabi	2014	0 (n=0) *	0 (n=0) *
Two Part	Kervashe	2013	100 (n=1)	0 (n=0)
	Heringe	2013	0 (n=0) *	0 (n=0) *
	Kervashe	2014	8 (n=1)	92 (n=12)
	Heringe	2014	0 (n=0)	100 (n=4)
	Hurabi	2014	25 (n=5)	75 (n=15)

* represents cases where no *Mecopoda* males of the particular song type could be found

However, the fact that there were differences among sympatric song types in their rate of parasitization suggests that there could still be a coevolutionary relationship between the tachinid flies and their host. In this study, we found evidence that Two Part has a higher probability of parasitization than the other two song types. It is interesting to note that the mating calls of Two Part has both chirp and trill component while Double Chirper and Helicopter calls consist of only chirp or trill components, respectively. In another study of two closely related bush cricket species of the genus *Poecilimon* that have calls differing in the number of syllables in chirps, it was found that the parasitoid *T. leonidei* parasitized the *Poecilimon* species with polysyllabic three to four times more often than the monosyllabic species (Lehmann and Heller 1998). A study by Wagner (1996) indicates that tachinid parasitoids find it easier to locate hosts with more call components. If parasitization is indeed a strong selection pressure on *M. elongata* Two Part populations, it is possible that the Two Part population split into Double Chirper and Helicopter song types with each retaining only one of the two components of Two Part call and both having a lower rate of parasitization.

Since 2010, field collections of *M. elongata* have been done at various times post monsoon (starting from September when mating season is about to start) from sites around Kadari field station. At our collection sites, the *M. elongata* breeding season begins at the end of September or the start of October. However, most tachinid infection, when it was discovered and studied in 2013 and 2014, appeared to occur at the end of the *M. elongata* mating season in February and March. *M. elongata* individuals collected before February were unaffected by parasitization. This suggests that the tachinid parasitoid life cycle lags that of the *M. elongata* reproductive cycle in Kervashe, Hurabi, and Heringe by four months. This trend was also seen in *Ormia ochracea* (Paur and Gray 2011); presumably the parasitoids are able to survive the *M. elongata* non-breeding season either through diapause or through exploiting an alternative host, although which of these life-history strategies it employs remains to be determined.

Parasites have long been acknowledged to be a potentially important factor for both sympatric and allopatric divergence of host species leading to host speciation. However, there is limited direct evidence of parasitism leading to host diversification (Buckling and Rainey 2002). *M. elongata* song types are a promising system that could throw light on the role of parasites in speciation.

Acknowledgements

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